

Cambrian Pelecypoda (Mollusca)

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Abstract: The record of Cambrian bivalved organisms that have been placed in the Mollusca includes undoubted pelecypods and other bivalved shells. This record is reviewed herein. Additional topotype material of Delgado's (1904, *Communicacoes da Commissao do Servico Geologico de Portugal* 5:307-374) Lower Cambrian specimens from Portugal shows that they are distorted brachiopods. Restudy of Zhang's (1980a, *Bulletin Chinese Academy of Geological Sciences*, Series 8, 1:1-19; 1980b, 26th International Geological Congress 4:121-129) type specimens from the Lower Cambrian of China shows that most of them are also brachiopods. New specimens of *Tuarangia* MacKinnon indicate that this genus is a Middle-Upper Cambrian pelecypod.

Key Words: Cambrian, Pelecypoda, Brachiopoda, *Fordilla*, *Pojetaia*, Mollusca, bivalves

Over the past generation, a great deal of new information and data have been added to our knowledge of Cambrian and Ordovician pelecypods; much of this new information is summarized by Babin in this volume. My paper concentrates on the expanding knowledge of Cambrian pelecypods.

Undoubted Cambrian pelecypods are now known from North America, Europe, Greenland, Asia, Africa, and Australia. However, the stratigraphic range of the class in the Cambrian, which bivalved taxa are pelecypods and which ones are not, and how the Cambrian pelecypods are related to Ordovician taxa, are all questions under study by various workers who have reached differing conclusions.

Much recent work in Europe and South America has shown that the great Ordovician radiation of pelecypods began in Arenigian time about 10 million years sooner than previously thought. Thus, it is reasonable to assume that Cambrian rocks hold part of the key to understanding Ordovician pelecypods.

The Ordovician radiation causes us to debate the number of subclasses of pelecypods that should be recognized. However, by the end of Ordovician time almost all modes of life exploited by pelecypods were present — deposit feeding, filter feeding, epifaunal byssal attachment, burrowing, semi-infaunal byssal attachment, nestling, boring and, probably, swimming; ligament types and dentition were also highly varied.

EARLY CAMBRIAN TAXA

The known Cambrian stratigraphic range of pelecyp-

pods is being filled in with records now ranging from the Early Cambrian through the early Late Cambrian.

In a previous summary of information about Cambrian pelecypods to that date (Pojeta, 1975) I came to the conclusion that the only undoubted Cambrian pelecypod was *Fordilla troyensis* Barrande, 1881 (Fig. 1A,C,D). I noted that *Lamellodonta simplex* Vogel, 1962, probably was an obolellid brachiopod, a decision later confirmed by Havlicek and Kriz (1978). In the 1975 paper, I gave the age of *Fordilla* as Early Cambrian. More recently, Geyer and Streng (1998:87) indicated the age of *Fordilla* as "early late Early Cambrian to the late Early Cambrian (probably equivalents of the Siberian Atdabanian and Boto-man[ian]..." Runnegar and Pojeta (1992:117) indicated *Fordilla* was known from rocks as old as Tommotian in Siberia (Fig. 2).

My 1975 summary noted that *Fordilla* was known from Lower Cambrian rocks in New York State, Newfoundland, Denmark, and Greenland. The genus has subsequently been found in Lower Cambrian rocks of the Siberian platform (Krasilova, 1977, 1987; Jermak, 1986) and eastern Germany (Elicki, 1994); Geyer and Streng, (1998:88) suggested that the German *Fordilla* could be better assigned to *Pojetaia*. In addition, undescribed material is known from Labrador.

The interpretation of *Fordilla* as a pelecypod was based on articulated material and internal molds that show pelecypod muscle scars. Subsequently, teeth and ligament groove fillings have been found (Pojeta, 1978). Subsequent workers accepted *Fordilla* as a pelecypod, documented the constancy of the muscle scar patterns, provided data about

Fordilla's shell microstructure, and added information about its geographic distribution in Early Cambrian time (Runnegar and Pojeta, 1992; Hinz-Schallreuter, 1995; Cope, 1996; Geyer and Streng, 1998; Cope and Babin, 1999).

Yochelson (1978) treated *Fordilla* as having originated from a hypothetical unknown ancestral mollusk sepa-

rately from the origin of the Pelecypoda from the same ancestor. Yochelson (1981) preferred to treat *Fordilla* as molluscan *incertae sedis*, until more information about the genus became known. The authors cited herein have provided that new information.

The other undoubted Early Cambrian pelecypod is *Pojetaia runnegari* Jell, 1980 (Fig. 1E-H), first described

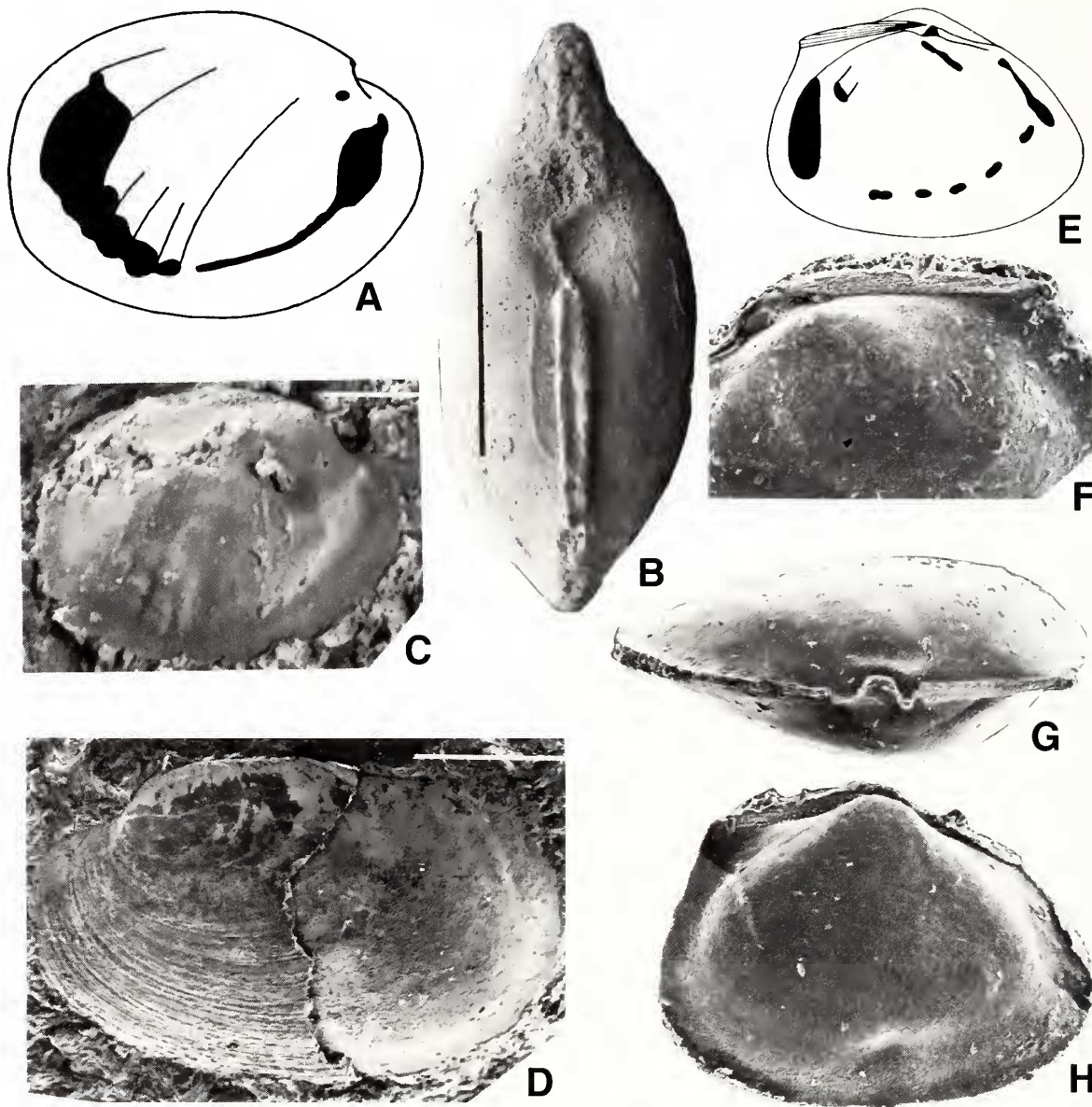


Fig. 1. Lower Cambrian pelecypods *Fordilla troyensis* Barrande (A, C, D), *F. siberica* Krasilova (B), and *Pojetaia runnegari* Jell (E-H). All scale bars equal one millimeter. **A**, right valve composite drawing of the muscle scars as seen on internal molds. Drawing by B. Runnegar. **B**, dorsal view of internal mold showing trace of one tooth in each valve and the filling of the ligament space, Lower Cambrian, Siberia. **C**, right valve internal mold showing most of the muscle scars, Lower Cambrian rocks, New York. **D**, left valve of partially shelled specimen showing growth lines, Lower Cambrian, Greenland. **E**, composite reconstruction of the muscle scars, modified from Runnegar and Bentley (1983); published with permission of *The Journal of Paleontology*. **F**, dorsal part of left valve showing ligament area and teeth, specimen 1 mm long, Lower Cambrian, Australia. **G**, dorsal view of internal mold showing trace of one tooth in each valve, anterior to left, specimen 1.2 mm long, Lower Cambrian, Australia. **H**, right lateral view of internal mold. The apparent texture on the surface was interpreted (Runnegar and Bentley, 1983) as impressions of crystals on the inner surface of the shell, specimen 0.9 mm long, Lower Cambrian, Australia.

from the Lower Cambrian rocks of Australia. This species was intensively studied by Runnegar and Bentley (1983), who dealt with all aspects of its morphology from prodissoconch I to shell microstructure. Runnegar and Pojeta (1992) added some information about comparative shell microstructure, stratigraphic distribution, and probable synonyms of both *Pojetaia* and *Fordilla*. *Pojetaia* has been widely accepted as the second well-documented Early Cambrian pelecypod. The genus is now known from Lower Cambrian rocks in South Australia; New South Wales, Australia; Anhui Province, China; Henan Province, China; Bornholm, Denmark; Morocco (Geyer and Streng, 1998); and, questionably from Newfoundland (Landing and Westrop, 1998). Geyer and Streng (1998:89) provided a table comparing the six named species of *Pojetaia*. Runnegar and Pojeta (1992:117) noted that *Fordilla* and *Pojetaia* are about coeval in their known first occurrences.

The relationships of *Pojetaia* and *Fordilla* to each other and to Ordovician pelecypods have been under frequent discussion. Making comparisons to Ordovician pelecypods, Pojeta and Runnegar (1985) regarded *Pojetaia* as a palaeotaxodont and *Fordilla* as an isofilibranch. Runnegar and Pojeta (1992) placed the two genera in a monophyletic grouping, Fordillidae Pojeta, 1975, based on their similar shell microstructure. Hinz-Schallreuter (1995) followed Runnegar and Pojeta (1992) and placed *Pojetaia* in the Fordillidae. Geyer and Streng (1998) and Cope (1996) treated *Pojetaia* as a palaeotaxodont. Cope (1996) noted that most authorities regard *Fordilla* as a pelecypod, but he doubted its assignment to the Isofilibranchia, as did Waller (1998). Cope and Babin (1999:175) noted: "Prolonged debate on the affinities of the genus *Fordilla*...has finally been settled and it is now regarded as one of the two known early Cambrian bivalve genera."

Runnegar and Pojeta (1992) and Geyer and Streng (1998) discussed the various Lower Cambrian taxa that have been assigned to the Pelecypoda. They noted probable synonyms and taxa that are probably not pelecypods. Herein, new information is provided on two occurrences, in Portugal and China, indicating that certain Lower Cambrian bivalves once regarded as pelecypods should be assigned elsewhere.

From the Lower Cambrian rocks of Portugal, Delgado (1904) described nine species, placed in six genera, of what he regarded as pelecypods. For years since his publication, Delgado's material was little studied or noticed. Teixeira (1952) restudied Delgado's material, placed three of the species defined by Delgado in "Lamellibranchia?," and the remainder in the single species "*Modiolopsis*" *bocagei* Delgado, which Teixeira regarded as a pelecypod.

In 1904, Delgado sent C. D. Walcott identified topotype specimens of *Modiolopsis bocagei* and *Davidia doll-*

fusi Delgado; these are figured herein for the first time (Fig. 3G, H). These specimens are probably deformed brachiopods; they clearly show cardinalia in the presumed brachial valves at the midlength of the hinge margin indicating a possible articulate brachiopod (identified by J. T. Dutro, Jr., who suggested that the cardinalia could be called socket ridges in these specimens). Thus, it seems likely that all of Delgado's "species" of Early Cambrian pelecypods are deformed brachiopods; the other elements of the fauna described by Delgado are also clearly deformed.

Zhang (1980a, b) described four new genera, seven new species, and two new families of bivalved creatures; these were first proposed as *nomina nuda* (Zhang, 1979). His material is from the Tianheban Formation, a *Redlichia* trilobite-bearing Lower Cambrian unit at Zhongbao Village, Xianfeng County, Hubei Province, China; Zhang treated the bivalves from Hubei as pelecypods. Zhang (pers. comm., June 1996) noted that the Hubei fauna may correlate with

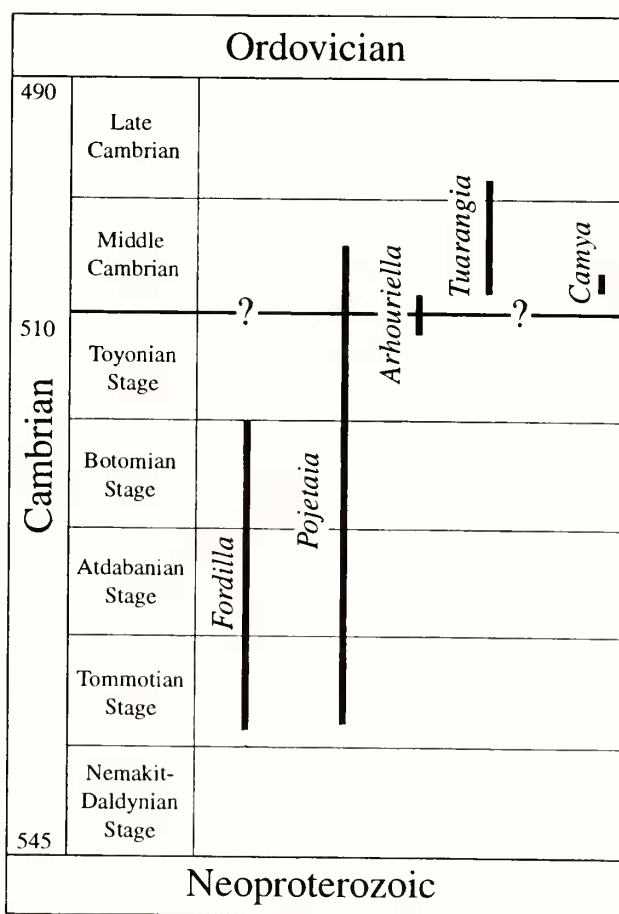


Fig. 2. Stratigraphic distribution of Cambrian pelecypods. The numbers in the left hand column indicate millions of years ago. The Early-Middle Cambrian boundary is queried because there is debate about where to place it (Landing *et al.*, 1998; Geyer, 1998).

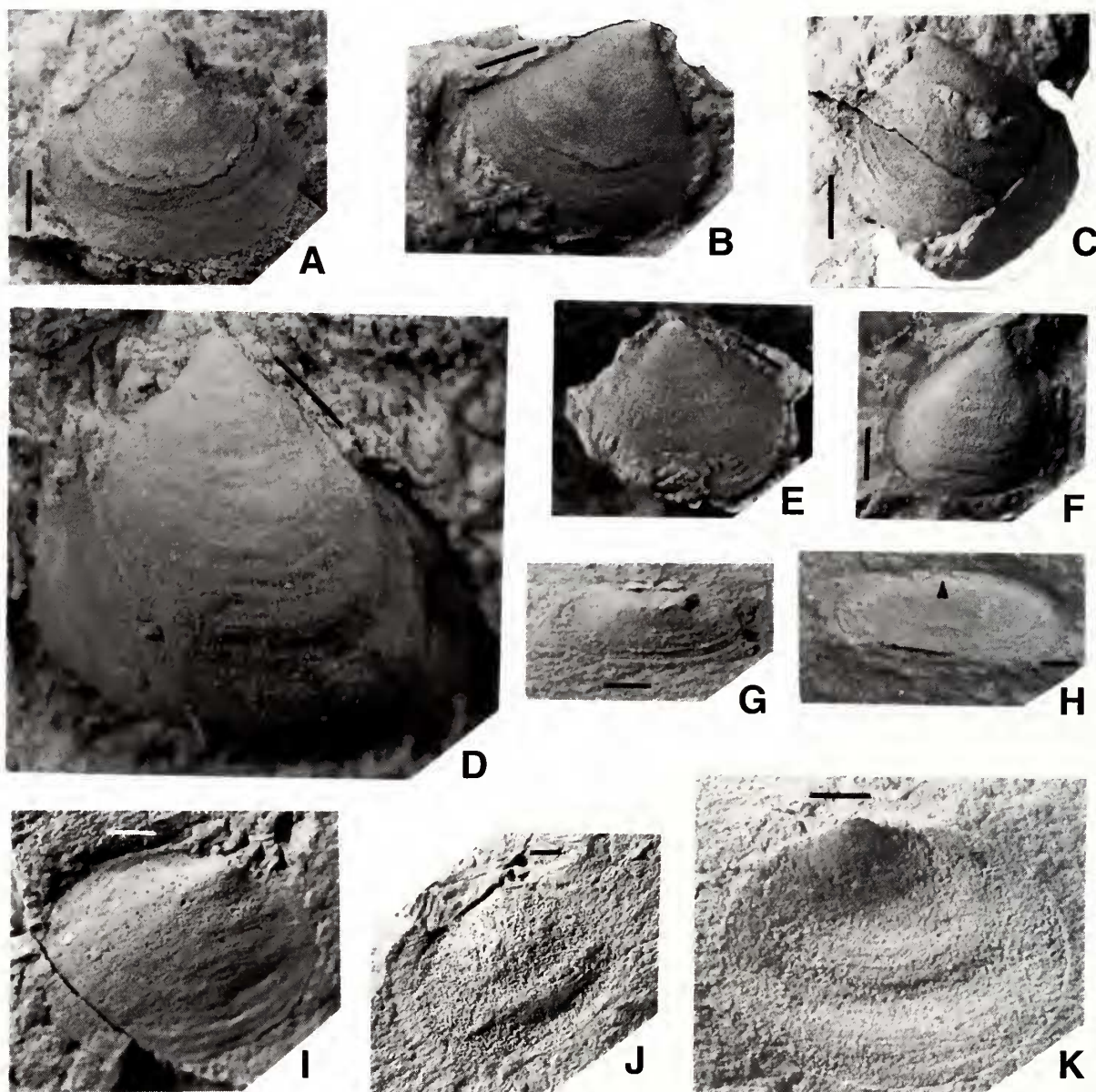


Fig. 3. Probable Lower Cambrian brachiopods that have been described as pelecypods. *Hubeinella formosa* Zhang (A-F), "*Davidia*" *dollfusi* Delgado (G), "*Modiolopsis*" *bocagei* Delgado (H), and *Xianfengoconcha minuta* Zhang (I-K). All scale bars represent 1 mm. A, paratype, figured by Zhang (1980a, pl. 3, fig. 3). B, paratype, figured by Zhang (1980a, pl. 3, fig. 4). C, paratype, figured by Zhang (1980a, pl. 3, fig. 2). D, holotype, figured by Zhang (1980a, pl. 3, fig. 1). E, previously unfigured specimen. F, paratype, figured by Zhang (1980a, pl. 3, fig. 5). A-F all from Lower Cambrian, China. G, H, symmetrical internal molds. Arrow points to apex of shell, which to either side has socket ridges. G and H are from Lower Cambrian, Portugal. I, holotype, figured by Zhang (1980a, pl. 2, figs. 12, 13). J, paratype, figured by Zhang (1980a, pl. 2, fig. 14). K, paratype, figured by Zhang (1980a, pl. 2, fig. 15). I-K are from Lower Cambrian rocks, China.

the Siberian Botomian Stage.

Subsequent to Zhang's work, Runnegar and Pojeta (1992) treated his taxa as stenothecoids, a group of uncertain affinities, and Geyer and Streng (1998:87) in discussing Zhang's taxa noted: "...the interpretation of the following taxa, all from the Early Cambrian of Hubei Province on the Cambrian Yangtze Platform, is refused: ...

All of them are based on slightly or considerably distorted valves of inarticulate brachiopods rather than pelecypods."

A difficulty in using Zhang's work is the low printed quality of the photographic illustrations. I have had the opportunity to examine and photograph many of his specimens (Figs. 3A-F, I-K, 4, 5).

Hubeinella formosa Zhang (1980a, pl. 3, figs. 1-5;

1980b pl. 1, figs. 20-21; Fig. 3A-F herein), the type and only known species of *Hubeinella*, has a near teardrop shape and prominent comarginal ornament similar to stenothecoids (Horný, 1957; Koneva, 1976, 1979). However, such a shape also occurs in obolellid inarticulate brachiopods. Some specimens of *Hubeinella* (Fig. 3B, D, E) show faint radial external ornament, a feature that occurs in obolellids but is absent in stenothecoids (Yochelson, 1969). Unfortunately, nothing is known of the internal features of *Hubeinella*.

Of *Xianfengoconcha* Zhang, I was able to restudy and photograph three specimens of *X. minuta* Zhang (1980a, pl. 2, figs. 13-15; 1980b, Plate 1, figs. 13, 14; Figs. 3I-K, 4A herein). All three specimens are poorly preserved molds that show nothing beyond an inequilateral shape and faint coarse and fine comarginal ornament. *X. minuta* is one of three species placed in *Xianfengoconcha* by Zhang; his figures of *X. elliptica* Zhang, type species of the genus, and *X. rotunda* Zhang are no more informative than the specimens of *X. minuta*.

Zhang (1980a:10) provided a drawing of the hinge of *X. elliptica* that shows an elongate toothlike structure on each side of the beak. Such structures occur in obolellid brachiopods (Rowell, 1965:292-293) including *Lamel-lodonta* Vogel (Havlicek and Kriz, 1978). In any case, these teeth do not show well on Zhang's plate, and most of the specimens of *X. elliptica* and *X. rotunda* figured by him are essentially equilateral in shape.

The most that can be said about *Xianfengoconcha* is that the known specimens are of a bivalved creature that shows no diagnostic pelecypod features, and which probably is an inarticulate brachiopod.

I have been able to examine and photograph four specimens (including the holotype) of *Praelamellodonta elegans* Zhang, the type species of *Praelamellodonta* (Zhang, 1980a, pl. 1, figs. 1, 3, 8, 12, 13; 1980b, pl. 1, figs. 1, 3, 5; Fig. 4B-H herein). The specimens range from a composite mold to one that is mostly covered with shell. The shape of the specimens varies as does the strength of the posterior umbonal slope, both of which suggest deformation of the original shape; the specimen shown in Figure 4H is clearly deformed.

The holotype of *Praelamellodonta elegans* (Fig. 4D, E) has a prominent beak to either side of which is a bladelike structure, and at least three specimens preserve some radial ornament (Fig. 4C, G, H). The bladelike structures to either side of the beak and the presence of radial ornament suggest that the specimens of *P. elegans* are distorted inarticulate brachiopods.

Thus, restudy of Zhang's specimens of *Hubeinella*, *Xianfengoconcha*, and *Praelamellodonta* reinforces the suggestion of Geyer and Streng (1998) that they are distorted valves of inarticulate brachiopods.

In addition to the above three genera, Zhang described the genus *Cycloconchoides* (Fig. 5A-D). He defined two species, *C. venustus* Zhang, the type species of the genus, and *C. elongatus* Zhang. I have examined and photographed four specimens including the holotypes of both species.

All the known specimens of *Cycloconchoides* preserve the shell and have a gross ornament of comarginal growth lines and radial ribs. No internal features are known. The growth lines are prominently raised and seem to truncate the radial ribs before the next set of ribs is formed. The general appearance of the specimens is that of a series of stacked shells such as occur in some arthropods that do not completely molt the old carapace. This is a prominent feature of conchostracan brachiopods some of which have radial ribs between the growth increments (Tasch, 1969). This type of ornament is not common in pelecypods and is not known to occur in any Cambrian or Ordovician species. However, brachiopods are not known from Lower Paleozoic rocks, and most brachiopods occur in fresh or brackish waters. Other bivalved arthropods are known from the Cambrian, such as *Canadaspis perfecta* (Walcott) (Conway Morris *et al.*, 1982); although *Canadaspis* does not stack its molts. Determining the affinities of *Cycloconchoides* will depend on finding new material that shows diagnostic features; specimens in which the shell is partially decorticated would be the most useful. It is unlikely that *Cycloconchoides* was either a pelecypod or a brachiopod.

MIDDLE AND UPPER CAMBRIAN TAXA

Recently, Middle Cambrian species of *Pojetaia* were described from Bornholm, Denmark (Hinz-Schallreuter, 1995) and Morocco (Geyer and Streng, 1998) (Fig. 2).

Geyer and Streng (1998) described the genus *Arhouria* from the early Middle Cambrian Jbel Wawrmast Formation of Morocco (Fig. 6C). *A. ophiodontoides* Geyer and Streng is known from two silicified incomplete presumed right valves. The species is roughly equilateral. Except for the hinge, internal features are poorly preserved; the authors (Geyer and Streng, 1998:93) noted that: "...the presence of a faint imprint interpreted as posterior adductor muscle scar [called anterior muscle scar in their fig. 7H]...Faint pallial [sic] commences at adductor muscle scar." These features are not readily apparent on their photographic figures and are not included on their reconstruction.

One specimen of *A. ophiodontoides* preserves a well-developed slightly concave hinge plate and some of the presumed posterior ligament area, which partly covers

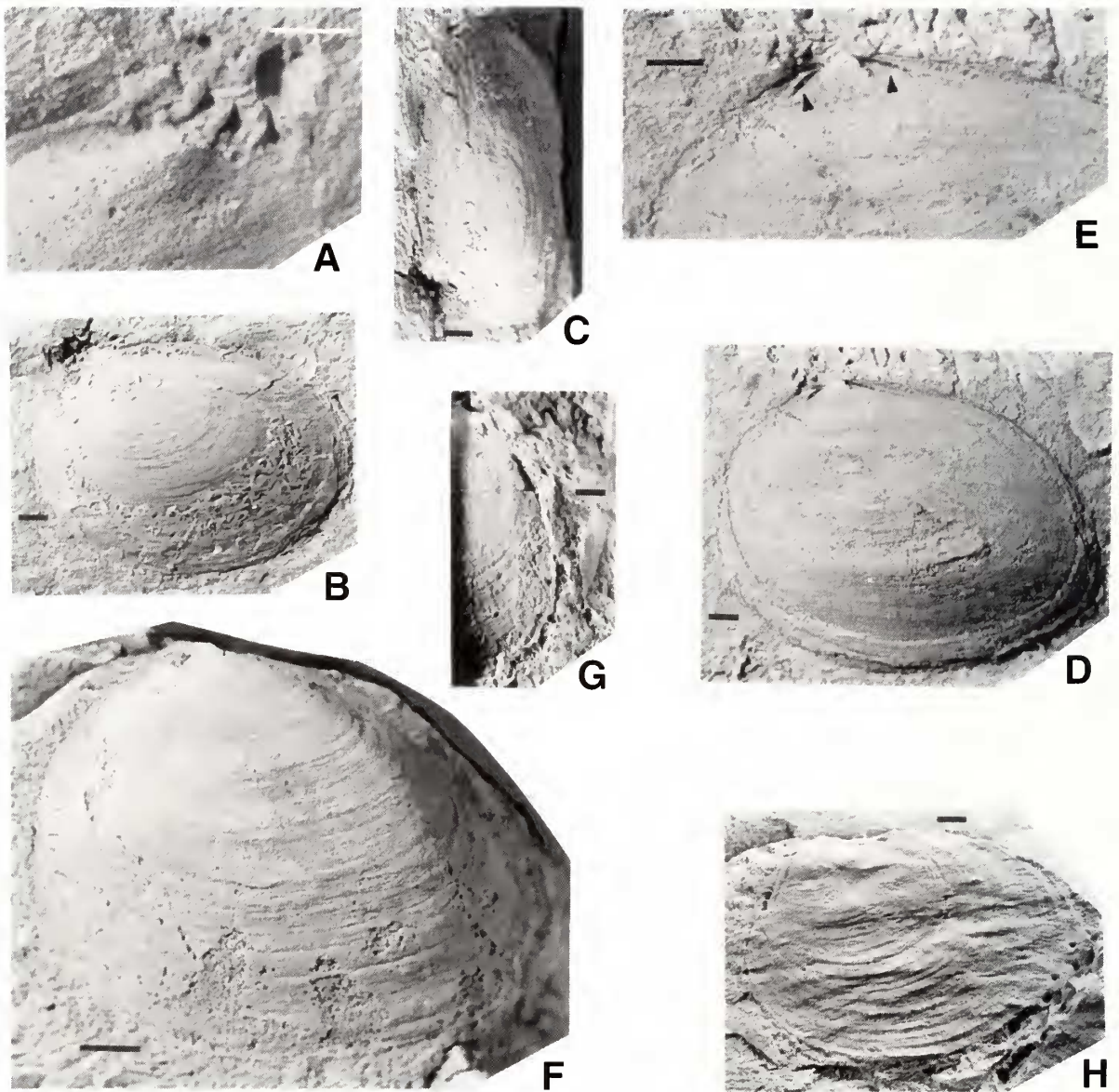


Fig. 4. Probable Lower Cambrian brachiopods from China that have been described as pelecypods. All bar scales represent 1 mm. *Xianfengoconcha minuta* Zhang (A) and *Praelamellodonta elegans* Zhang (B-H). **A**, enlargement of apical area of specimen shown on Fig. 3I. **B**, **C**, paratype, C shows some radial ribbing, figured by Zhang (1980a, pl. 1, fig. 8). **D**, **E**, holotype, E is an enlargement of the apical area, arrows point to bladelike structures to either side of the apex, figured by Zhang (1980a, pl. 1, fig. 1). **F**, **G**, paratype, G shows some radial ribbing, figured by Zhang (1980a, pl. 1, figs. 12, 13). **H**, distorted paratype showing radial ribbing, figured by Zhang (1980a, pl. 2, fig. 3).

the hinge plate (Fig. 6C). The hinge plate undercuts the two pronglike central teeth. Anterior to the teeth there is an elongate fossette that Geyer and Streng interpret as an additional ligament area; they reckon that the ligament extended over the entire hinge plate in an early ontogenetic stage. The anterior of the two teeth originates directly on the dorsal margin and not on the hinge plate.

If *Arhouriella ophiodontoides* is a pelecypod, and if the amphidetic interpretation of its ligament is correct, it is

clearly very different from *Fordilla* and *Pojetaia* which have opisthodetic ligaments.

John C. W. Cope (pers. comm., September 1999) suggested that the teeth of *Arhouriella ophiodontoides* could best be compared to those of the Upper Cretaceous solemyoid *Nucinella sohli* Pojeta (1988, pl. 5). Leaving aside the fact that the oldest known nucinellid is Early Jurassic in age, a major dentition difference between the two species is that in *N. sohli* the peglike teeth are mounted

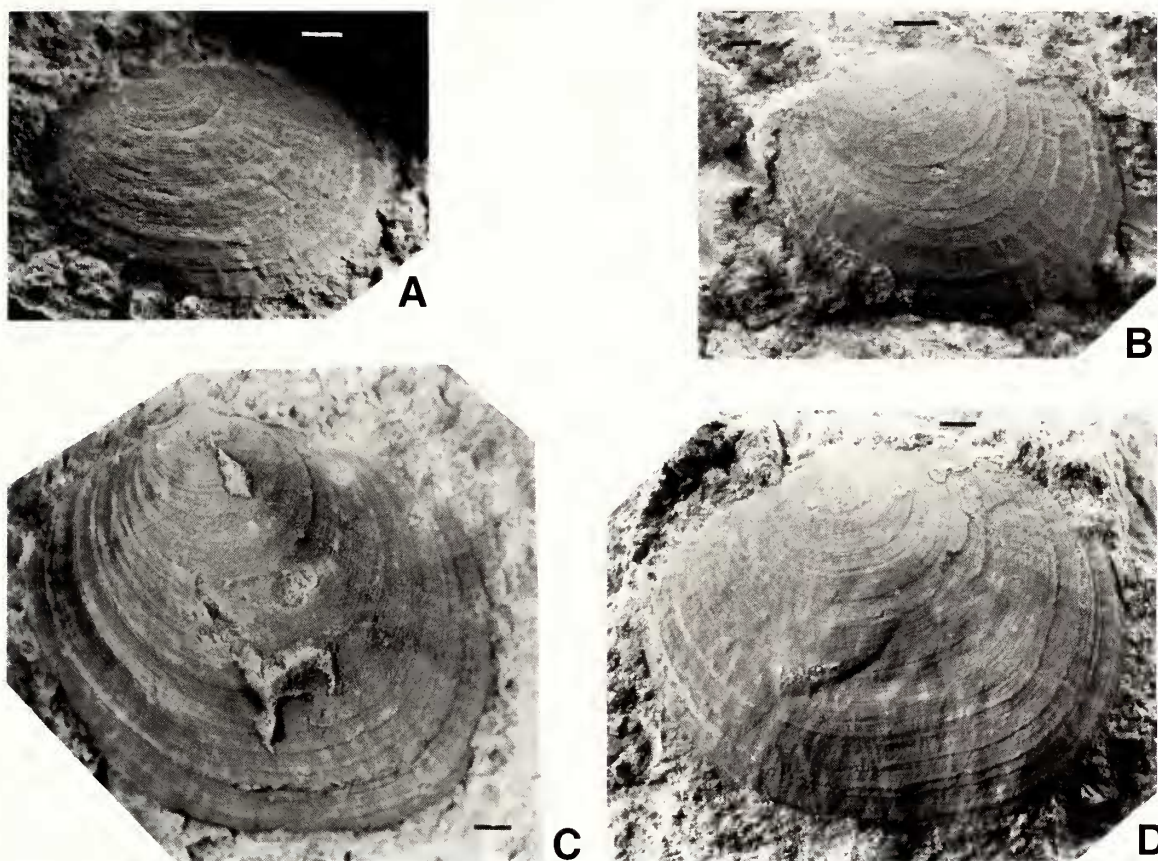


Fig. 5. *Incertae sedis* Lower Cambrian bivalves from China: possible arthropods. *Cycloconchooides elongatus* Zhang (A), and *C. venustus* Zhang (B-D). All scale bars represent 1 mm. A, holotype, figured by Zhang (1980a, pl. 3, fig. 14). B, paratype, figured by Zhang (1980a, pl. 3, fig. 8). C, paratype, figured by Zhang (1980a, pl. 3, fig. 9). D, holotype, figured by Zhang (1980a, pl. 3, fig. 6).

directly on the hinge plate, and, as in other solemyoids, *N. sohli* is anteriorly elongated.

Clearly, Geyer and Streng have a very unusual bivalve and additional specimens will help determine its systematic position.

Tuarangia paparua MacKinnon (1982) was first described from the Middle Cambrian Tasman Formation of New Zealand; the species is based on at least one hundred specimens. Subsequently, Berg-Madsen (1987) described *T. gravgaerdensis* from the Middle Cambrian Andrarum Limestone of Bornholm, Denmark.

Tuarangia (Fig. 6A, D-E) has been the subject of much discussion as to whether or not it is a pelecypod, and, if it is, how it is related to other pelecypods. MacKinnon (1982) placed *Tuarangia* in the Pteriomorphia with question, even though the genus possesses numerous taxodont teeth. He interpreted its shell microstructure as foliated calcite, which he noted in pelecypods occurs only in the Pteriomorphia. He also noted that the genus has an amphidetic ligament that shows as a raised ridge, between the two rows of taxodont teeth on internal molds.

Runnegar (1983) regarded *Tuarangia* as being related to the "quasiostroconch" *Pseudomyona queenslandica* (Runnegar and Jell), because both have foliated calcite shell microstructure, and he interpreted the presumed amphidetic ligament of *Tuarangia* as representing the place where a univalved protoconch had broken off from the rest of the shell. *Pseudomyona* is known to have a univalved protoconch and a bivalved adult shell. Runnegar thought of *Tuarangia* and *Pseudomyona* as bivalved monoplacophorans. Carter (1990:179) noted: "The order Tuarangioida is, therefore, presently regarded as a monoplacophoran derivative which is convergent toward the Bivalvia." Waller (1998:10) regarded *Tuarangia* as being poorly known and noted its various taxonomic placements.

With conviction, MacKinnon (1985) placed *Tuarangia* firmly in the Pteriomorphia and disassociated it from *Pseudomyona* by noting that the middorsal ridge on internal molds was the underside of an amphidetic ligament. The ridge between the rows of taxodont teeth is preserved in the same way on all known specimens, and he noted that there is no sign that it represents a broken-off

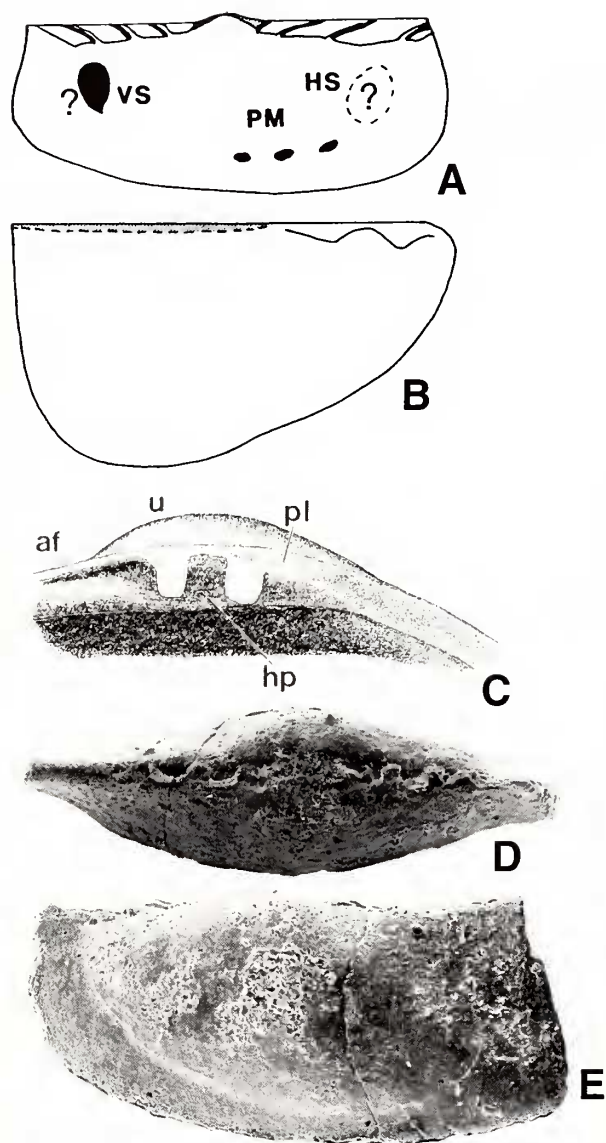


Fig. 6. Middle and Upper Cambrian pelecypods. *Tuarangia gravgaerensis tenuiumbonata* (A), *Camya asy* (B), *Arhouriella opheodontoides* (C), and *Tuarangia paparua* (D, E). A, reconstruction of muscle scars from Hinz-Schallreuter (1995:75); VS = anterior adductor, HS = posterior adductor, PM = pallial line. B, drawing of shape and dentition from Hinz-Schallreuter (1995:75). C, drawing of hinge from Geyer and Streng (1998:93); af = anterior fossette, u = umbo, pl = posterior ligament area, hp = hinge plate. D, E, dorsal and left lateral views, specimen 0.9 mm long. Figures A and B reproduced with permission of *Geschiebekunde aktuell*. Figure C reproduced with permission of *Revista Española de Paleontología*.

structure. Berg-Madsen (1987) maintained the placement of *Tuarangia* in the Pteriomorphia, but with reservations. She also figured *Tuarangia* sp. from an erratic boulder from Poland; the boulder contained Upper Cambrian conodonts, which indicate that *Tuarangia* ranged into lower Upper

Cambrian. Runnegar and Pojeta (1992) maintained the close association of *Tuarangia* and *Pseudomyona*, based on similar shell microstructure, and separated them from the lineage including *Fordilla* and *Pojetaia*.

Hinz-Schallreuter (1995) described a pelecypod faunule from the Middle Cambrian Exsulans Limestone of Bornholm, Denmark. The faunule contains *Pojetaia ostseensis*, *Tuarangia gravgaerensis tenuiumbonata*, and *Camya asy*, all named by Hinz-Schallreuter in her 1995 paper.

In discussing *Tuarangia gravgaerensis tenuiumbonata*, Hinz-Schallreuter noted that she had complete shells showing both the interior and exterior and that they have a space for an amphidetic ligament as interpreted by MacKinnon (1982, 1985). Her description of this species noted the presence of pallial muscles and an anterior adductor muscle (Fig. 6A). These features do not show well where she notes their presence on her figure 5.3. The muscles are shown on her reconstruction (Hinz-Schallreuter, 1995:75) where the position of the anterior adductor muscle scar is in black and queried. She indicated the possible position of the posterior adductor muscle with a dashed open circle within which is a question mark; in her description she noted that the posterior adductor muscle was not preserved on her material. If Hinz-Schallreuter's interpretation of the musculature of *Tuarangia* proves correct, there is no doubt that it is a Cambrian pelecypod and is not related to *Pseudomyona*, because that genus has a single sub-central muscle. Cope and Babin (1999) accepted Hinz-Schallreuter's reconstruction of *Tuarangia*.

Hinz-Schallreuter also defined the Middle Cambrian pelecypod genus *Camya*, type species *C. asy*. This species (Fig. 6B) is like *Tuarangia* in its anterior-posterior elongation and long dorsal margin, but it is more constricted anteriorly; the beaks are in an anterior position, and there is a single tooth to either side of the beak. The species is known from two left valves that show comarginal growth lines. Other features of the species are unknown.

Babin (1993) has shown that the supposed Middle Cambrian pelecypod from Belgium, *Modiolopsis ? malaisii* Fraipont, 1910, is a pseudofossil.

Pojeta (1980:77) figured an unnamed possible Late Cambrian pelecypod from the Frederick Limestone of Maryland. This specimen shows only shell shape; no other specimens have been found, and its status as a pelecypod remains dubious.

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